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Ontogenic changes in the feeding ecology of the early life stages of the Antarctic silverfish (*Pleuragramma antarcticum*) documented by stable isotopes and diet analysis in the Dumont d'Urville Sea (East Antarctica)

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Abstract

The feeding ecology of the notothenioid fish *Pleuragramma antarcticum* was studied in the Dumont d'Urville Sea (East Antarctica) near the French Antarctic station. Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and diet contents were used in order to study dietary shifts between fish larvae and juveniles. All specimens had low $\delta^{13}C$ values ($<-24‰$), a main characteristic of high-Antarctic pelagic species. Fish larvae showed differences in both carbon and nitrogen ratios when compared with juveniles. Muscle $\delta^{15}N$ values showed a difference of one trophic level ($\sim 3‰$) between larvae (6.7‰) and juveniles (9.7–10.0‰) and a trophic position of tertiary consumers. Diet content analyses (stereomicroscope and scanning electron microscopes) indicated that larvae are omnivorous, feeding on phytoplankton (mainly diatoms) as well as on zooplankton species. A positive relationship between $\delta^{15}N$ values and size was found and indicated a carnivorous diet for older specimens.

Keywords: $\delta^{13}C$; $\delta^{15}N$; Southern Ocean; Trophic relationships; Omnivory

1. Introduction

Pleuragramma antarcticum, also known as the Antarctic silverfish, is the most abundant pelagic fish species in the high-Antarctic shelf waters of the

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Southern Ocean (Hubold, 1984). Its entire life cycle is pelagic with a long larval phase of over one year. Spawning is thought to occur in late winter–early spring with eggs hatching in November–December (Koubbi et al., 2011; Vacchi et al., 2004). Larvae are found throughout the water column but are more abundant in the upper water layers (~200 m), while juveniles and adults are often distributed at greater depths (Granata et al., 2009). This spatial segregation pattern is probably an important feature to avoid intraspecific competition (Hubold, 1985) and ensures the survival of the species. *P. antarcticum* acts as a direct link between herbivorous/omnivorous mesozooplankton and higher levels of the trophic web because it is consumed by a variety of predators such as birds, fish and marine mammals (Cherel, 2008; Eastman, 1985; Koubbi et al., 2009; La Mesa et al., 2004). Along with krill species, this micronektonic species has a mid-trophic level that might exert a "wasp-waist control" in the neritic Antarctic ecosystem with a top–down control on mesozooplankton and a bottom–up control on top predators (Cury et al., 2000).

Biologists have long relied upon gut content analysis to investigate predator–prey interactions (Hysop, 1980) as this approach gives a "snapshot" on prey items eaten at a particular time. From this method, *P. antarcticum* larvae have mostly been documented as feeding on zooplankton species, mainly copepods (Granata et al., 2009; Hubold and Hagen, 1997; Kellermann, 1987; Takahashi and Nemoto, 1984) but also on phytoplankton (Koubbi et al., 2007; Vallet et al., 2011), while juveniles have been documented as feeding upon copepods, euphausiids, amphipods and even chaetognaths (Hubold, 1985; Hubold and Ekau, 1990). An indirect approach using the stable isotope method has also been used over the past 30 years to elucidate patterns in food-webs. The value of this application is the fact that stable isotopes ratios of consumers reflect those of their diet in a predictable manner (Fry, 1988; Hobson and Clark, 1992; Rau et al., 1982; Wada et al., 1987). Carbon and nitrogen isotope compositions ($\delta^{13}C$ and $\delta^{15}N$) differ between organisms and their prey because of a selective retention of heavy isotopes and excretion of the light isotopes (Michener and Schell, 1994). Because stable isotopes dynamics are a long-term process, the stable isotope ratio in tissue reflects the diet over a period from weeks to months, depending on the protein turnover rate of the analysed tissues (Tieszen et al., 1983). In the case of fish muscle samples, this temporal integration is estimated to be amount to several days to months depending on fish growth rates (Herzka, 2005).

Stable-carbon signatures ($\delta^{13}C$) vary little along the food chain, approximately 0.8‰ per trophic level (Minagawa and Wada, 1984; Owens, 1987) and are mainly used to indicate the foraging habitats of predators, including fish. Carbon values have been used to characterize fish habitat in marine ecosystems and discriminate between inshore/benthic species from offshore/pelagic species (Cherel et al., 2011; Pinnegar and Polunin, 2000). In estuarine ecosystems, $\delta^{13}C$ values differentiate fish from the upper, middle and lower zones of the estuary (Pasquaud et al., 2008; Riera and Richard, 1996) and are also a useful tool to investigate fish movements and migrations (Bardonnet and Riera, 2005; Limburg, 1998). Stable-nitrogen signatures ($\delta^{15}N$) are mainly used to establish trophic relationships (Hobson and Montevecchi, 1991; Hobson and Welch, 1992; Rau et al., 1982). These results support the generalization that, on average, a 3‰ enrichment in $\delta^{15}N$ values accompanies each trophic step (DeNiro and Epstein, 1981; Garcia et al., 2007; Michener and Schell, 1994; Peterson and Fry, 1987; Tieszen and Boutton, 1989). This enrichment could be explained by the fractionation of nitrogen isotopes during the production of ammonia, urea or uric acid. ^{14}N is preferentially excreted (Minagawa and Wada, 1984) and consequently, a high ratio of nitrogen isotopes indicates a high trophic position (Hobson and Welch, 1992).

The Antarctic silverfish probably undergoes ontogenic changes in diet, and may therefore occupy a number of trophic levels in the course of their life history, as demonstrated for other fish species (Polis and Strong, 1996). Also from otolith analysis, *P. antarcticum* is believed to have a planktonic existence for the early part of its life, and then to switches to an offshore pelagic life style (Radtke et al., 1995). Food resource partitioning was documented between larval and one year old juvenile using gut content analysis (Kellermann, 1987) demonstrating that both developmental stages fed on different size fractions of zooplankton with negligible overlap. Zooplankton taxa that have been documented as part of the diet of *P. antarcticum* were considered in this study as potential prey. Other Antarctic species such as chaetognaths, jellyfish and polychaetes have been documented as carnivorous (Froneman and Pakhomov, 1998) and were studied as potential competitors for *P. antarcticum*. By combining gut content and stable isotope approaches the authors wanted to determine (1) diet shifts between *P. antarcticum* larvae and juveniles, (2) the trophic

position of larvae and juveniles and their relationship in the East Antarctic food-web ecosystem, and (3) finally, whether larvae and juveniles foraging in different habitats as suggested by previous analysis.

2. Materials and methods

2.1. Sampling

Samples were collected in the Dumont d'Urville Sea (East Antarctica) during the international CEA-MARC surveys (Collaborative East Antarctic Marine Census) of the Census of Antarctic Marine Life and the French IPEV-ICO^{2}TA programme (Integrated Coastal Ocean Observations) in Terre Adélie.

Fish samples were collected during the austral summer 2007–2008 from the Japanese TRV *Umitaka Maru* using pelagic trawls (International Young Gadoid Pelagic Trawl, IYGPT, and Rectangular Midwater Trawl, RMT). Samples were collected at nine stations along a transect from the Mertz Glacier Tongue (MGT) to the Adélie Bank. Stations 10–12 and 24–27 were used for gut content analysis and stations 10–13, 24 and 42 for stable isotopes (Fig. 1). Fish were sorted and identified on board and measured to the nearest 0.1 mm with a digital caliper (standard length, SL) at the laboratory before analysis. *P. antarcticum* up to 30 mm SL were considered as larvae and individuals between 30 and 100 mm SL as juveniles (Kellermann, 1987; Koubbi et al., 2011). Samples were kept in 70% ethanol for stable isotope analysis and in 5% buffered formalin for gut content analysis. Potential prey (phytoplankton, copepods, euphausiids, and amphipods), competitor species (jellyfish, chaetognaths, polychaetes) and some *P. antarcticum* larvae ($n = 15$) were collected with the French RV *l'Astrolabe* in January 2010 with an Isaacs-Kidd Midwater Trawl (IKMT), bongo nets and WP2 nets. Zooplankton

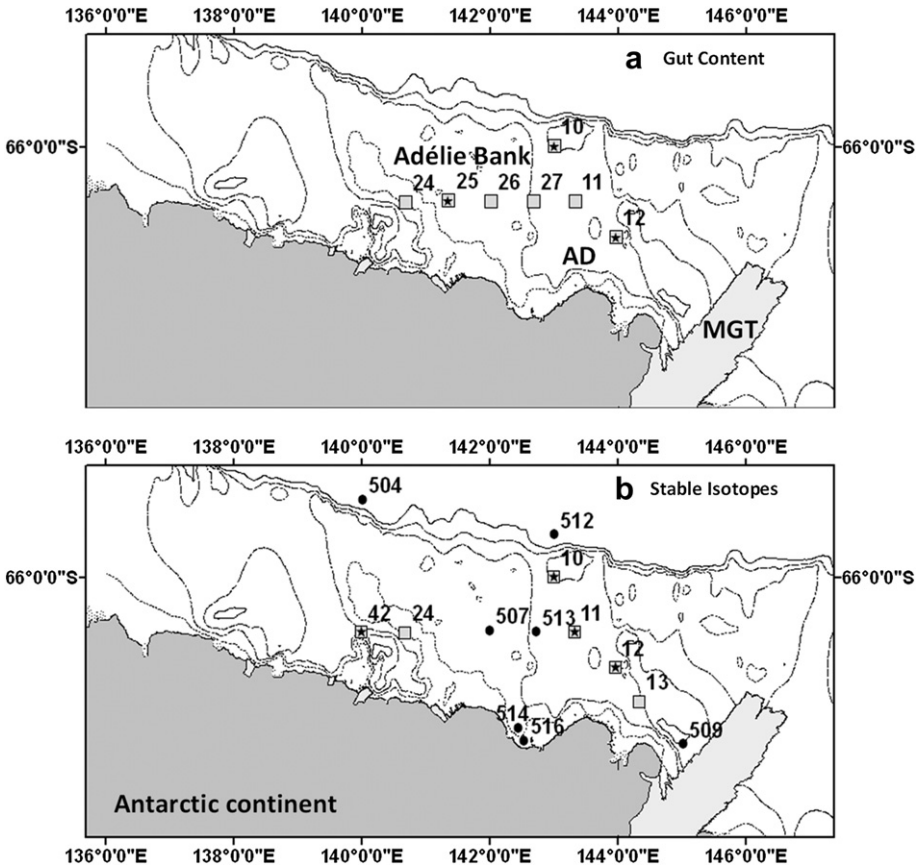

Fig. 1. Sampling stations during the cruises of the *Umitaka Maru* in 2008 and *l'Astrolabe* in 2010. Sampling stations for (a) gut content (10–42) and (b) stable isotopes analysis (504–516). Larvae are represented by squares, and juveniles by black stars. Zooplankton species are represented by black points. AD = Adélie Depression. MGT = Mertz Glacier Tongue.

were kept in 70% ethanol. For phytoplankton, water from a depth of 5 m was collected with Niskin bottles in January 2010 and filtered on Whatman type F glass-fiber filters pretreated at 450 °C for several hours and stored frozen at −80 °C until analysis.

2.2. Stable isotopes analysis

The isotopic signatures of *P. antarcticum,* phytoplankton, zooplankton prey and competitor species were determined with different preparations depending on the analysed tissue. For *P. antarcticum*, a total of 144 specimens from different size classes and from six sampling stations were studied. Lateral muscle samples were removed from juveniles ($n = 76$) and whole specimens were used for larvae ($n = 68$). Because of the small size of some zooplankton organisms like the copepods *Paraeuchaeta antarctica*, the chaetognath *Eukrohnia hamata* and some *P. antarcticum* larvae, two to 10 individuals were pooled together (Table 1).

All samples were dried for at least 36 h at +50 °C and grounded to a fine powder. Following Cherel et al. (2011) lipids were extracted using cyclohexane. The C:N is related to lipid content in animal tissues (Post et al., 2007). Because lipids are depleted in ^{13}C when compared to proteins and carbohydrates (DeNiro and Epstein, 1978; Tieszen et al., 1983) delipidated samples allowed comparing the carbon isotopic signature without any deleterious effect due to different lipid contents among individuals and species. C:N values <4 indicate low lipid contents that do not influence the $\delta^{13}C$ signatures (Post et al., 2007). Copepod, euphausiid, pteropod and amphipod samples

Table 1
Fish and zooplankton sampling from the *Umitaka Maru* (2008) and *l'Astrolabe* (2010) cruises for stable isotope analysis.

	Stable isotopes				
Species	*n*	SL (mm)	Tissue	Sampling stations	Date (jj/mm/yyyy)
Fish					
Pleuragramma antarcticum					
Small larvae (*l'Astrolabe*)	15	10.1 ± 0.6	Whole body (five larvae pooled)	AS 508 (St. 12)	13/01/2010
				AS 516	21/01/2010
Larvae (*Umitaka Maru*)	53	19.1 ± 2.5	Whole body	10–13, 24, 42	06/02/2008–11/02/2008
Juveniles (*Umitaka Maru*)	76	74.3 ± 15.0	Muscle	10–12, 42	06/02/2008–11/02/2008
Potential prey species *(l'Astrolabe)*					
POM (Phytoplankton)	3	–	Filters	AS 507	12/01/2010
				AS 514	19/01/2010
				AS 516	21/01/2010
Amphipod					
Themisto gaudichaudii	1	16.8	Whole body	AS 504	11/01/2010
Copepods					
Paraeuchaeta antarctica	10	~10	Whole body (pooled)	AS 512	17/01/2010
Euphausiid					
Euphausia crystallorophias					
Larvae	3	9.9 ± 0.4	Whole body	AS 513	17/01/2010
Juveniles	3	30 ± 0.2	Whole body	AS 513	17/01/2010
Mollusc					
Thecosomes pteropods	6	17.1 ± 1.4	Whole body	AS 504	11/01/2010
Gymnosome pteropods	1	8	Whole body	AS 504	11/01/2010
Competitors (*l'Astrolabe*)					
Chaetognath					
Eukrohnia hamata	3	47.6 ± 1.8	Whole body (pooled)	AS 504	11/01/2010
Sagitta gazellae	4	80.9 ± 1.0	Whole body	AS 504	11/01/2010
Cnidarian					
Jellyfish	1	–	Tentacle	AS 512	17/01/2010
Jellyfish	1	–	Tentacle	AS 509	14/01/2010
Jellyfish	1	–	Tentacle	AS 508	13/01/2010
Siphonophores	3	24.7 ± 0.4	Whole body	AS 504	11/01/2010
Polychaete					
Tomopteris sp.	1	81.2	Small fraction	AS 512	17/01/2010

were acidified afterwards with 1N HCl to remove carbonates from their exoskeleton. Carbonates were also removed from the phytoplankton filters using fuming HCl. Additionally, a small fraction of the filters was observed under an inverted microscope revealing that most of the items were diatoms, with no zooplankton species found in the analyzed fraction. Once lipids and carbonates had been extracted, samples were dried again for several hours.

Relative abundance of ^{13}C and ^{15}N were determined using an Isoprime (Micromass) continuous-flow isotope-ratio mass spectrometer. Stable isotope concentrations are expressed in delta (δ) notation and calculated as:

$$\delta X = \left[\left(\frac{R\ \text{sample}}{R\ \text{standard}}\right) - 1\right] \times 1000$$

where $X = {}^{15}N$ or ^{13}C and R is the corresponding ratio $^{15}N{:}^{14}N$ or $^{13}C{:}^{12}C$. R standard for ^{13}C and ^{15}N are the PDB (PeeDee belemnite) standard and atmospheric N_2, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors $<0.15‰$ for $\delta^{13}C$ and $<0.20‰$ for $\delta^{15}N$.

Trophic level (TL) was calculated using the equation proposed by Wada et al. (1987) for Antarctic ecosystems:

$$TL = 1 + \frac{\delta^{15}\text{Nanimal} - \delta^{15}\text{Nalgae}}{3.2}$$

where TL is the trophic level of a consumer, δ^{15}Nanimal is the $\delta^{15}N$ value of the consumer's tissue (‰) and δ^{15}Nalgae is the $\delta^{15}N$ value of phytoplankton. The value 3.2 is the mean $\delta^{15}N$ increases in fish muscle proposed by Sweeting et al. (2007).

2.3. Gut content analysis

The gut contents of 54 larvae (stations 10–12, 24–27) and 15 juveniles (stations 10, 12, 25) (Fig. 1a) were analysed. The whole digestive tract was removed from fish under a stereomicroscope and opened. Larger prey were identified with a stereomicroscope and microplankton were identified with Scanning Electron Microscope (SEM). For SEM, food items of each specimen were rinsed with Milli-Q water (Millipore) and filtered on 0.2 μm filter (Millipore polycarbonate) which was put on a carbon tape attached to a metal stub (25 mm diameter) according to Vallet et al. (2011). Stubs were dried under laminar flow hood during 24 h and then palladium–gold-coated (Polaron SC7620) and observed with a LEO SEM (438VP). Microplankton genus identification was made according to Scott and Marchant (2005). Some prey items were not identified to the species level, owing to their advanced state of digestion; they were therefore referred to as unidentified diatoms, dinoflagellates or eggs.

Observations were coded as presence/absence and the number of species present in gut (n) was calculated. The frequency of occurrence ($\%F$) was designed as follows:

$$\%F = \left(\frac{Si}{S}\right) \times 100$$

where Si is the number of individuals in which the species i was present and S the total number of individuals analysed.

2.4. Statistical analysis

Spatial variability in stable isotopes results for larvae and juveniles was tested using Kruskal–Wallis and Kolmogorov–Smirnov tests. For fish larvae, only stations with more than 5 specimens were tested (stations 10–12, 24). Stations 13 and 42 had very few larvae individuals and were not taken into account for this part of the analysis. Juveniles were collected in four samples (stations 10–12, 42), with more than 15 individuals at each of them, hence all sampling stations were tested.

3. Results

3.1. Size classes

Fish were between 8.7 and 95.8 mm SL. The size class distribution of larvae collected in 2008 and 2010 were significantly different (Kolmogorov–Smirnov test, $P < 0.05$) with an average standard length (SL) of 10.1 ± 0.6 mm for individuals collected in 2010 and of 19.1 ± 2.5 mm SL for those collected in 2008. For comparison, samples from 2010 are referred in this study as "small larvae" and samples from 2008 only as larvae. Juveniles had an average SL of 74.3 ± 15.0 mm.

3.2. Stable isotope analysis

3.2.1. Pleuragramma antarcticum

Nitrogen values ranged from 7.2‰ for fish larvae to 10.1‰ for fish juveniles (Fig. 2, Table 2). There was no significant difference in $\delta^{15}N$ values between "small

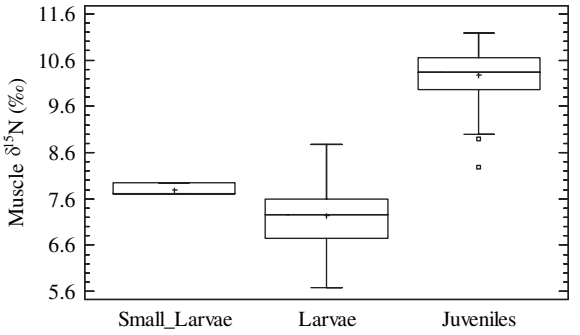

Fig. 2. Nitrogen isotopic signature of early life stages of *P. antarcticum*. The upper and lower bars of the box represent the first and third quartiles, respectively. Therefore, the length of the box equals the interquartile range (IQR). The horizontal line inside the box indicates the location of the median. Vertical lines are drawn from each side of the box and extend to the most extreme observations that are no farther than 1.5 IQRs from the box. Observations farther than 1.5 IQRs from the box are shown as individual points.

larvae" and larvae (Mann-Whitney-Wilcoxon test, $W = 3.17$, $P > 0.05$). Juveniles were segregated from larvae stages (Kruskal–Wallis test, $H = 96.3$ $P < 0.05$) with a difference of $\sim 3‰$ in $\delta^{15}N$ values reflecting one trophic level of difference between these developmental stages.

A positive relationship was also found between length (SL, mm) and $\delta^{15}N$ of *P. antarcticum* (logarithm regression model, coefficient of regression 2, correlation coefficient 0.90, $R^2 = 81.6$, Fig. 3). The following equation is derived from the model:

$$\delta^{15}N = 1.5 + 2 \times \mathrm{In}\,(SL)$$

Carbon values were low for all specimens; $\delta^{13}C$ ranged from -26.4 to $-23.4‰$, with larvae having the greatest range of values compared to juveniles. Average $\delta^{13}C$ values were $-25‰$, $-26.6‰$ and $-25.3‰$ for small larvae, larvae and juveniles, respectively. A significant difference was found between "small larvae" and larvae in $\delta^{13}C$ values (Mann-Whitney-Wilcoxon test, $W = -60.5$, $P < 0.05$) (Fig. 4, Table 2). Larvae were also segregated when compared to juveniles and small larvae simultaneously (Kruskal–Wallis test, $H = 25.75$, $P < 0.05$) (Fig. 4, Table 2).

There was a significant difference in $\delta^{13}C$ values between sampling stations reflecting spatial variability, for both larvae (Kruskal–Wallis test, $H = 32.41$, $P < 0.05$) and juveniles (Kruskal–Wallis test, $H = 26.28$, $P < 0.05$).

3.2.2. Potential prey and competitor species

The isotopic signature of potential prey and competitor species is summarized in Table 2.

Table 2
Isotopic signature of *Pleuragramma antarcticum,* potential prey and competitor species. Values are given as X ± SD in ‰. Three different but unidentified species of jellyfish were analyzed, the AS (number) refer to *l'Astrolabe* cruise and the sampling station.

Species	Age	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	C:N
POM (Phytoplankton)		2.0 ± 0.2	−29.5 ± 0.2	5.4 ± 0.2
Fish				
Pleuragramma antarcticum	Small larvae	7.8 ± 0.1	−25.0 ± 0.0	3.2 ± 0.0
	Larvae	7.2 ± 0.4	−26.6 ± 0.7	3.1 ± 0.0
	Juveniles	10.1 ± 0.4	−25.3 ± 0.2	3.2 ± 0.0
Potential prey species				
Amphipods				
Themisto gaudichaudii	Adults	9.2	−26.2	3.7
Copepods				
Paraeuchaeta antarctica	Adults	10.2	−25.6	3.5
Euphausiids				
Euphausia crystallorophias	Juveniles	6.9 ± 0.1	−24.4 ± 0.0	3.5 ± 0.0
Euphausia crystallorophias		6.4 ± 0.2	−27 ± 0.1	4.1 ± 0.0
Molluscs				
Thecosomes pteropods	–	4.3 ± 0.6	−25.7 ± 0.4	3.6 ± 0.0
Gymnosome pteropods	–	6.2	−25.0	3.5
Competitors				
Chaetognaths				
Eukrohnia hamata	–	−25.5 ± 0.0	8.1 ± 0.1	3.3
Sagitta gazellae	–	−24 ± 0.8	9.2 ± 0.5	3.2 ± 0.0
Cnidarians				
Jellyfish (AS 512)	–	−24.0	8.9	3.3
Jellyfish (AS 509)	–	−24.0	9.3	3.0
Jellyfish (AS 508)	–	−24.4	5.3	3.0
Siphonophores	–	−23.9 ± 0.4	6.6 ± 0.9	3.1

The nitrogen isotopic signature of phytoplankton from water samples was 2.8‰. For zooplankton species, nitrogen values enclosed a 5.9‰ difference and ranged from 4.3‰ for thecosome pteropods (*Clio* sp.) to 10.2 for the large copepod *Paraeuchaeta antarctica*. The euphausiid *Euphausia crystallorophias* and gymnosome pteropods had average values around 6‰. The amphipod *Themisto gaudichaudii*, and the chaetognaths *Sagitta gazellae* and *E. hamata* had all $\delta^{15}N$ values >8‰ and jellyfish had $\delta^{15}N$ values from 5.3 to 9.3‰. Nitrogen values were significantly different between species (Kruskal–Wallis test, $H = 25.70$, $P < 0.05$).

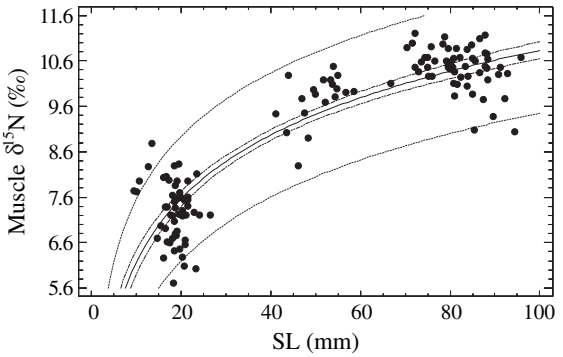

Fig. 3. Logarithm regression model between $\delta^{15}N$ and standard length (SL). The plot shows the least squares regression line and two sets of limits. The inner limits provide 95% confidence intervals. The outer dotted lines are 95% prediction limits for new observations.

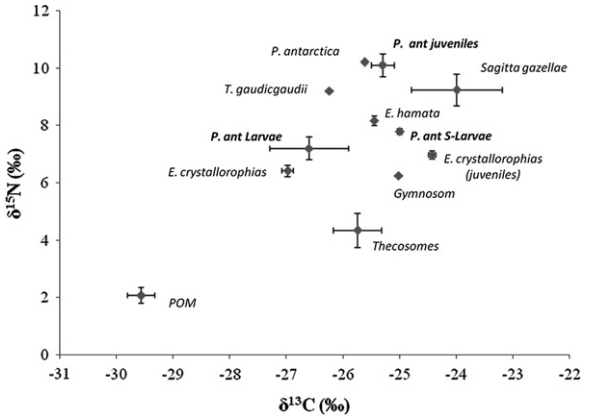

Fig. 5. Isotopic signature of *P. antarcticum* and of its potential prey. Values are means ± sd.

Average carbon values of phytoplankton were −29.5‰. Zooplankton species enclosed a 2.3‰ $\delta^{13}C$ difference from −26.2‰ for *T. gaudichaudii* to −23.9‰ for siphonophores. Two groups were segregated by $\delta^{13}C$: the first group had average $\delta^{13}C$ values around −24‰ (cnidarians, *S. gazellae, E. crystallorophias)* and the second group had average $\delta^{13}C$ values >24‰ (gymnosomes, *T. gaudichaudii*, thecosomes, *Paraeuchaeta antarctica* and *E. hamata*) (Kruskal–Wallis test, $H = 22.75$, $P < 0.05$) (Fig. 5).

Trophic levels (TL) ranged from 1.5 for herbivores thecosome pteropods *(Clio* sp.*)* to 3.2 for carnivorous species such as *P. antarcticum* juveniles or the copepod *Paraeuchaeta antarctica*. *P. antarcticum* larvae show a TL of 2.5 (Table 3).

3.3. Gut content analysis

A total of 69 *P. antarcticum* gut contents were analyzed. From the 54 gut contents of fish larvae only two were empty (less than 4%), and from the 15 juvenile's gut contents only one was empty (6.6%). In fish larvae, 23 taxa of phytoplankton, 2 taxa of zooplankton and 1 of protozoan were identified. Diatoms of the genus *Fragilariopsis* spp. and unidentified eggs were the most frequently prey observed, with 70.4% and 50.0% frequency of occurrence (%*F*), respectively. Another frequently encountered food items were diatoms of the genus *Chaetoceros* spp. and *Thalassiosira* spp., both with average values of 40%*F*. Copepods and dinoflagellates had average values >20%*F*.

For *P. antarcticum* juveniles, nine families of phytoplankton, some copepod species and unidentified

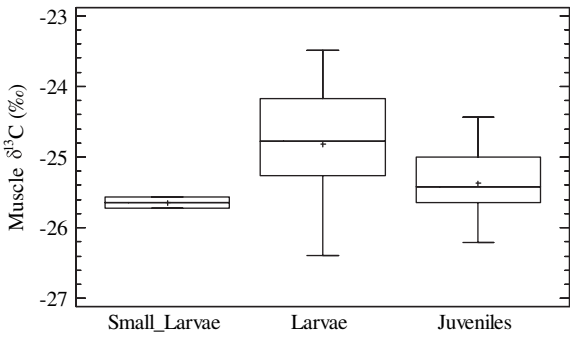

Fig. 4. Carbon isotopic signature of early life stages of *P. antarcticum*.

Table 3
Trophic level of Antarctic organisms.

	Trophic level (TL)	Organisms	TL values
1	POM	Phytoplankton (diatoms)	1
2	Herbivores, zooplankton	Thecosome pteropods *(Clio* sp.*)*	1.5
		Jellyfish AS 508	1.7
		Gymnosome pteropods	2.0
		Siphonophores	2.1
		Euphausia crystallorophias	2.4
		Euphausia crystallorophias (juvenile)	2.5
3	Carnivores, zooplankton	*P. antarcticum* larvae	2.6
		P. antarcticum larvae (small)	2.8
		Eukrohnia hamata	2.6
		Jellyfish AS 512	2.8
		Tomopteris sp.	2.9
		Themisto gaudichaudii	2.9
		Sagitta gazellae	2.9
		Jellyfish AS 509	3.0
		P. antarcticum Juveniles	3.2
		Paraeuchaeta antarctica	3.2

eggs were present. Some of the copepods that we were able to identify belong to the genera *Oithona* and *Oncaea* and to the Calaniidae family (Table 4). Diatoms of the genus *Fragilariopsis* spp. were still frequently encountered (66.6%*F*). Large copepods and planktonic eggs were found in 50–60% of the gut analyzed.

4. Discussion

4.1. Foraging habitat

Low $\delta^{13}C$ values in all developmental stages were characteristic of high-Antarctic pelagic species (Cherel, 2008; Zhao et al., 2004). Although slightly significant differences were found between sampling stations for each developmental stages, it was not clear whether these differences had an ecological meaning or if they were a sampling/analysis artefact since the number of fish samples varied for each station. It has been suggested that there is little variation in POM $\delta^{13}C$ signatures within a given water mass and abrupt changes at fronts (Cherel and Hobson, 2007). Stations 11 and 12 located close to the Adélie Depression, were significantly different by $\delta^{13}C$ values. Fish larvae were also segregated from juveniles and presented a greater range of $\delta^{13}C$ values. Larvae were found throughout the water column but were most abundant in surface waters while juveniles and adults were present only in deeper waters (Granata et al., 2009). As suggested by otolith analysis, *P. antarcticum* migrates into deeper waters as it matures and is thought to move between diverse hydrographic conditions (migration between inshore and offshore areas) (Radtke et al., 1995). Vertical and horizontal distribution patterns may be related to $\delta^{13}C$ variability, and a corresponding shift in diet suggests a different foraging habitat between larvae and older stages. Cherel et al. (2011) from the same study area show that $\delta^{13}C$ values of *P. antarcticum* adults were slightly higher in specimens caught near the bottom than the ones from pelagic trawls, which agrees with adult *P. antarcticum* living in the deep and occasionally feeding near the bottom (Eastman, 1985).

Table 4
Diet composition of *P. antarcticum* larvae and juveniles from gut content analysis observed with Scanning Electron Microscope. *%F* = Frequency of occurrence.

		Species	*%F* larvae ($n = 54$)	*%F* juveniles ($n = 15$)
Phytoplankton	Diatoms	*Actinocyclus* spp.	3.7	–
		Asteromphalus spp.	16.7	6.67
		Chaetoceros spp.	40.7	6.67
		Coccoliths	5.6	–
		Corethron pennatum	1.9	–
		Coscinodiscus spp.	1.9	–
		Cryptophyceae	3.7	–
		Eucampia spp.	1.9	–
		Fragilariopsis spp.	70.4	66.67
		Halsea sp.	1.9	–
		Nitzschia spp.	5.6	–
		Proboscia	1.9	–
		Pseudonitzschia spp.	1.9	–
		Rhizosolenia antennata	5.6	–
		Scrippsiella troichoidea	1.9	–
		Stellarima microtrias	3.7	–
		Thalassiosira spp.	38.9	13.33
		Thalassiothrix antarctica	7.4	13.33
		Trichotoxon spp.	18.5	13.33
		Unidentified Diatoms	7.4	–
	Dinoflagellates	Unidentified Dinoflagellates	22.2	13.33
	Choanoflagellates		5.6	–
	Nanoflagellates		1.9	–
	Protozoans		–	6.67
	Silicoflagellates	*Dictyocha speculum*	16.7	–
Zooplankton	Copepods	Calaniidae family	25.9	60.00
	Appendicularians		–	6.67
	Eggs		50.0	53.33
	Gasteropods	*Limacina* spp.	3.7	–

4.2. Trophic relationships

There was a positive relationship between length and $\delta^{15}N$ of *P. antarcticum*. Similar results have been found for other fish species and are often attributed to either ontogenic changes in diet or a differential metabolic fractionation of nitrogen isotopes with age (Melville and Connolly, 2003; Beaudoin et al., 1999). A difference of about 3‰ in $\delta^{15}N$ values between larvae and juveniles suggested one trophic level of difference between them. This hypothesis is supported by our results in gut content analysis and also by other methods such as lipid biomarkers. Fatty acids showed a strong omnivory for larvae, *Calanus* type markers for juveniles and euphausiid markers for older stages (Mayzaud et al., 2011). SEM and trophic level calculation showed that *P. antarcticum* larvae were omnivorous; the diet was not only composed of zooplankton (mainly copepods) but also phytoplankton species (mainly diatoms from the genus *Fragilariopsis*) as found by Vallet et al. (2011). The contribution of primary producer to the diet of fish larvae explains the lower $\delta^{15}N$ values when compared to juveniles or strictly carnivorous species. Even if some phytoplankton cells were still observed in the gut content of the juvenile, the larger zooplankton prey such as copepods (mainly calanoids up to 3 mm length), and chaetognaths were also frequently encountered. The isotopic signature of *P. antarcticum* adults from the same cruise is documented by Cherel et al. (2011). There were no differences in nitrogen values between juveniles and adults reflecting a carnivorous/zooplankton diet for older stages. The average $\delta^{15}N$ value of *P. antarcticum* juveniles/adults off Adélie Land (Cherel, 2008; Cherel et al., 2011; this study) was similar to the nitrogen signature of specimens collected in other regions of the Southern Ocean (Burns et al., 1998; Hodum and Hobson, 2000) suggesting no major differences in the foraging ecology of the species over all of the Antarctic shelf, as already suggested by Cherel (2008).

The zooplanktonic $\delta^{15}N$ values were in close agreement with diet composition documented from others approaches, such as gut content analysis or lipid biomarkers. Euphausiids have been extensively documented as part of the diet of *P. antarcticum* juveniles (Hubold, 1985; Hubold and Ekau, 1990; Kellermann, 1987; Takahashi and Nemoto, 1984). Lipid biomarkers (Mayzaud et al., 2011) suggest a gradual and increasing shift from a copepod dominant diet for young juveniles to a euphausiid dominant diet for older juveniles. The isotopic signature of the two dominant euphausiid species from the Adélie Land coastal waters (*E. crystallorophias* and *Euphausia superba*, this study and Cherel, 2008) reflects a herbivorous/omnivorous diet for both species. *E. crystallorophias* has been reported as being herbivorous when phytoplankton are abundant, but it has been suggested that it may efficiently switch to alternate food items such as copepods, ice algae or detritus. As *Calanus* type copepods are also herbivorous/omnivorous depending on the species, the isotopic signature of calanoids and euphausiids are probably similar explaining why there is no difference between juveniles and adults using the stable isotopes approach. This finding underlines one of the limits of this method, since two or more different prey species can have the same isotopic signature; thus precluding the specific identification of the prey.

The large copepod *Paraeuchaeta antarctica* showed the greatest $\delta^{15}N$ values. *Paraeuchaeta antarctica* has been reported to be a carnivorous species (Hopkins, 1987; Bocher et al., 2000) which is equipped with a pair of feeding appendages allowing it to capture smaller copepods and to rip pieces out of zooplankton organisms that are much larger than themselves (Michels and Schnack-Schiel, 2005). Some of the *Paraeuchaeta antarctica* documented prey were small species such as the copepods *Oncaea* spp. or *Microcalanus pygmaeus*, but also larger species such as *Metridia gerlachei*. *Paraeuchaeta antarctica* $\delta^{15}N$ values and trophic level (TL ~3) were almost identical to those of *P. antarcticum* juveniles and adults. Therefore, it seems unlikely that *Paraeuchaeta antarctica* could be a potential prey of *P. antarcticum* juveniles or adults since results suggested that these two species fed on prey within the same trophic level and could be considered as competitors.

The hyperiid amphipod *T. gaudichaudii*, is one of the most common pelagic amphipods of the Southern Ocean (Bocher et al., 2001). It has been recognized as an obligate carnivore and consumes mostly copepods, euphausiids and pteropods (Hopkins, 1985; Pakhomov et al., 1996). *T. gaudichaudii* had $\delta^{15}N$ values slightly lower than *P. antarcticum* juveniles or adults suggesting that it preys upon lower trophic level organisms. More recently, lipid biomarkers indicate that an indirect source of phytoplankton was present in the lipid signature of *T. gaudichaudii*. This observation may reflect that their food (such as salps) are herbivorous and support stable isotope results (Nelson et al., 2001).

Chaetognaths were documented as part of the gut content analysis of juveniles (Hubold, 1985; Kellermann, 1987) but they are also known as important predators, hence their classification here as

"competitors". The two dominant chaetognaths in our study area were *E. hamata* and *S. gazellae*. They have been documented to be opportunistic predators generally feeding on the most abundant prey, copepods. However, $\delta^{15}N$ values of these two species revealed a slight difference between them, suggesting that prey items from a greater trophic level are part of the larger *S. gazellae's* diet. Gut content analyses strengthened this hypothesis (Froneman and Pakhomov, 1998). While both species mainly prey upon copepods (mainly *Oithona* spp., *Calanus* spp. and *Rhincalanus gigas*), *S. gazellae* appeared to consume a wider variety of prey such as pteropods (*Limacina* spp.) and chaetognaths (Froneman et al., 1998) which could explain the $\delta^{15}N$ differences.

Jellyfish and siphonophores are carnivorous zooplankton species. Nitrogen values between 5.2 and 9.2‰ reflect important differences in diet composition among species. The $\delta^{15}N$ levels of *P. antarcticum* juveniles were generally similar to those of jellyfish, indicating that both groups occupied a similar trophic level within the pelagic ecosystem.

The plasticity in diet is an important feature to establish species' survival and responses to climate change. The existence of omnivory would facilitate adaptation of consumers to spatial and temporal variability of plankton (Tenore et al., 1995). The key role of *P. antarcticum* over the Antarctic shelf may be comparable to the role of other fish like anchovy or sardines in other regions, and myctophid fish in oceanic waters worldwide. The North Iberian sardine (*Sardina pilchardus)* had $\delta^{15}N$ values around 10–12‰ with no difference between juveniles and adults (Bode et al., 2004). These values were similar to those of *P. antarcticum* juveniles, but since a trophic baseline was not available in the European study, a direct comparison in terms of trophic level was difficult to establish.

5. Conclusion

The combination of fish gut content analysis and the measurement of stable isotopes were a powerful tool to examine dietary changes that occur during the ontogeny of the Antarctic silverfish. This study underlines the importance of using the two methods simultaneously, since each method provides a level of resolution that cannot easily be achieved by the other one (Clarke et al., 2005). Both approaches agree with a shift from omnivorous/herbivorous *P. antarcticum* larvae to a carnivorous/zooplankton diet for juveniles and adults. The trophic position among species was characterized by a continuum, with fish larvae and juveniles occupying the tertiary consumers level. $\delta^{13}C$ values were in agreement with high-Antarctic pelagic ecosystems, but it was unclear why fish larvae had a greater variability when compared to juveniles or adults. Larvae stages probably require greater flexibility in order to survive during this critical point of development.

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